Detrital feeding in *Xeniostoma inexpectans*, new genus, new species, and new subfamily Xeniostomatinae of Calliostomatidae (Gastropoda: Vetigastropoda), hosted by hexactinellid sponges of the Aleutian Islands, Alaska

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ABSTRACT

The new genus *Xeniostoma*, type species *X. inexpectans* new species, occurs from 200–400 m, off the western Aleutian Islands, Alaska, in association with vase-shaped hexactinellid sponges of the family Rossellidae. The feathery radula of *Xeniostoma* indicates an allocation to the Calliostomatidae. It is assigned to the new subfamily Xeniostomatinae because it lacks the massive inner marginal teeth that function in the carnivorous feeding of other genera in the family. There is no evidence of spongivory; its feathery teeth are suitable for feeding on detritus that accumulates on the host sponge.

Xeniostoma is also unusual in the family Calliostomatidae for its shell with rounded whorls, lack of spiral sculpture, large protoconch, and lack of teleoconch 1, its lack of jaws, and lack of the pseudoproboscis; it is also unusual in having a large right suboptic tentacle. The very large protoconch suggests that only a few large eggs are produced and that larvae can gain protection among the large projecting spicules on the outer surface of the host sponge. Within the Calliostomatidae, *Xeniostoma* most resembles the nearly smooth-shelled Magellanic genera *Photinula* Adams and Adams, 1854 and *Photinastoma* Powell, 1951, which have morphology of the lateral teeth in common and a similar shell profile, but have the other characters expected in carnivorous calliostomatids of the subfamily Calliostomatinae.

The typical subfamily Calliostomatinae exhibits an extreme level of specialization that sets it apart from other trochiform vetigastropods. If other living or fossil genera become known, there would be further support for the hypothesis that Xeniostomatinae could represent a surviving member of a nearly extinct basal group within Calliostomatidae.

One other trochiform vetigastropod family, the smaller-shelled Trochaclididae, is also hosted by deep-water hexactinellid sponges of the family Rossellidae. A reconsideration of the feathery radula of Trochaclididae leads to the conclusion that it too is suitable for detrital feeding.

Additional keywords: Calliostomatidae, Xeniostomatinae, Trochaclididae, Rossellidae, spongivory, Hexactinellid sponges

INTRODUCTION

Benthic sampling for resource-monitoring purposes has been conducted in recent years by the National Marine Fisheries Service in the vicinity of the Aleutian Islands, Alaska. New species of mollusks have been recognized by the late Rae Baxter and by Roger N. Clark; descriptions of further new species will be forthcoming.

Among the new findings is a remarkable new monotypic genus *Xeniostoma* and new species *inexpectans*, for which the smooth shell resembles the trochid genus *Margarites* in the subfamily Margaritinae, and the Magellanic genus *Margarella* in the subfamily Gibbulinae, but radular characters of the new genus are indicative of the family Calliostomatidae. Within the Calliostomatidae, the closest comparison in shell profile is with the Magellanic genera *Photinula* H. and A. Adams, 1854 and *Photinastoma* Powell, 1951, which have nearly smooth shells unlike those of most other calliostomatids. Comparisons are made in the descriptions of the new genus and species to the type species *Photinula coerulescens* (King and Broderip, 1831), from southern Argentina and Chile (Figures 9-11) and *Photinastoma taeniata* (Wood, 1850), from southern Argentina (Figures 12–13).

A number of questions about the affinity and its possible phylogenetic significance are raised by this discovery. The taxonomic question requires resolution by the placement in a new subfamily of Calliostomatidae. Another question of major interest concerns the association of the new species with hexactinellid sponges. This requires comparison with two other groups of trochiform gastropods that have previously been reported to occur on vase-shaped sponges of the family Rossellidae in the sponge order Hexactinellida. No information about this group of sponges has been provided in the accounts of the gastropods; this omission is addressed here with references to the literature on hexactinellid biology.

The best known gastropod family associated with hexactinellid sponges is the small-shelled trochiform vetigastropod family Trochaclididae Thiele, 1928, all members of which are known to be associated with hexactinellid sponges (Marshall, 1995b, and references therein). In previous reports on the Trochaclididae, there has been no information pertaining to the sponges.

Another species of comparable size and morphology identified by Gutt and Schicken (1998) as "*Margarella* sp." [likely *M. antarctica* Lamy, 1905], is also associated with hexactinellid sponges of the family Rosellidae in the Antarctic fauna. The genus *Margarella* Thiele, 1893, has most recently been assigned to the subfamily Gibbulinae of the Trochidae by Zelaya (2004).

The new calliostomatid genus *Xeniostoma* represents the third known vetigastropod group known to be associated with vase-shaped sponges of the order Hexactinellida.

Questions about the association of these gastropod families with the hexactinellid sponges are raised: Are these gastropods feeding directly on the sponges or are they feeding on detritus that accumulates on the sponges? What other benefits are derived from the association of these gastropods with the sponges?

MATERIALS AND METHODS

The new species has come to light due to collecting efforts of the late Rae Baxter and subsequently by Roger N. Clark, both of whom have obtained specimens in the process of salvaging invertebrate specimens from the trawl catches, while aboard survey vessels during summer cruises at the Aleutian Islands.

Specimens were preserved directly in ethyl alcohol of unknown strength, without relaxation or fixation. The preservation of all material for the new species is not adequate for thorough analysis. Preserved bodies of the specimens have been twisted out of the shell, but bodies of all specimens are torn, with the visceral mass not remaining attached to the head-foot. The head-foot material is suitable for study of the external anatomy and the radula; the macerated remains of the viscera are suitable for examination of gut contents, but not for determining the condition of the gonads.

Although none of the records of associated vetigastropods are accompanied by identified sponges, some information on the biology of the hexactinellid sponges is provided here. All three records (*Xeniostoma*, one species of *Margarella*, and all Trochaclididae) mention vase-shaped sponges, which are here noted to be members of the family Rosellidae. A substantial number of genera are known in the Rosellidae, based on the morphology of the siliceous spicules and the size and general morphology of the sponge (see Leys, et al. [1998], and Leys, et al. [2007] for general review of hexactinellid biology).

Abbreviations: F/V, Commercial fishing vessel contracted for survey cruises, by National Marine Fisheries Service; LACM, Natural History Museum of Los Angeles County; USNM, United States National Museum of Natural History, Washington; SEM, Scanning electron microscopy.

SYSTEMATICS

Superorder Vetigastropoda Salvini-Plawen, 1980
Superfamily Trochoidea Rafinesque, 1815

Family Calliostomatidae Thiele, 1924

Remarks: Hickman and McLean (1990) and Hickman (1996) previously treated the group Calliostomatinae as a subfamily of Trochidae, but other recent authors including Marshall (1995a), Warén and Bouchet *in* Bouchet and Rocroi (2005), Williams et al. (2010), have treated this as a full family, as done so here. The most current and comprehensive taxonomic treatment is that of Marshall (1995a), who provided a complete list of generic level taxa of Calliostomatidae. Marshall distinguished two subfamilies in which the sculpture consists of beaded spiral cords, typical Calliostomatinae and Thysanodontinae Marshall, 1985, members of which have a completely different radula of slender teeth with backward directed barbs. Thysanodontinae are not further mentioned here. A third subfamily Xeniostomatinae is proposed here.

Subfamily Calliostomatinae Thiele, 1924

Diagnosis: Spiral sculpture of raised cords, usually strongly beaded; protoconch diameter usually relatively small (diameter 320–420 μm); protoconch with raised hexagonal pattern and apertural rim; short teleoconch I of first quarter whorl; pseudoproboscis well developed; jaws well-developed; inner marginal teeth of radula enlarged.

Remarks: The typical subfamily was further divided into two tribes by Marshall (1995a), the typical Calliostomatini and Fautricini Marshall, 1995, the latter with shell characters not unlike Calliostomatini, but considered by Marshall to exhibit a basal, plesiomorphic condition of the radula for the family.

Subfamily Xeniostomatinae new subfamily

Diagnosis: Profile low, spiral sculpture lacking at all growth stages; protoconch smooth, very large (900 μm); teleoconch I lacking; pseudoproboscis lacking; jaws lacking; inner marginals not enlarged.

Included Genera: Monotypic for *Xeniostoma*, new genus. Other species or genera may await discovery.

Remarks: The lack of enlarged inner marginal teeth distinguish this subfamily from typical members of the subfamily Calliostomatinae. The lack of any spiral sculpture, the lack of jaws, and the lack of the pseudoproboscis are further differences from Calliostomatinae.

Xeniostoma new genus

Type Species: *Xeniostoma inexpectans* new species, by original designation.

Description: Generic level description as in species description below.

Remarks: The genus is monotypic; once additional species become known, the limits of the genus will be better understood; differences in size at maturity, shell proportions, and shell sculpture can be expected.
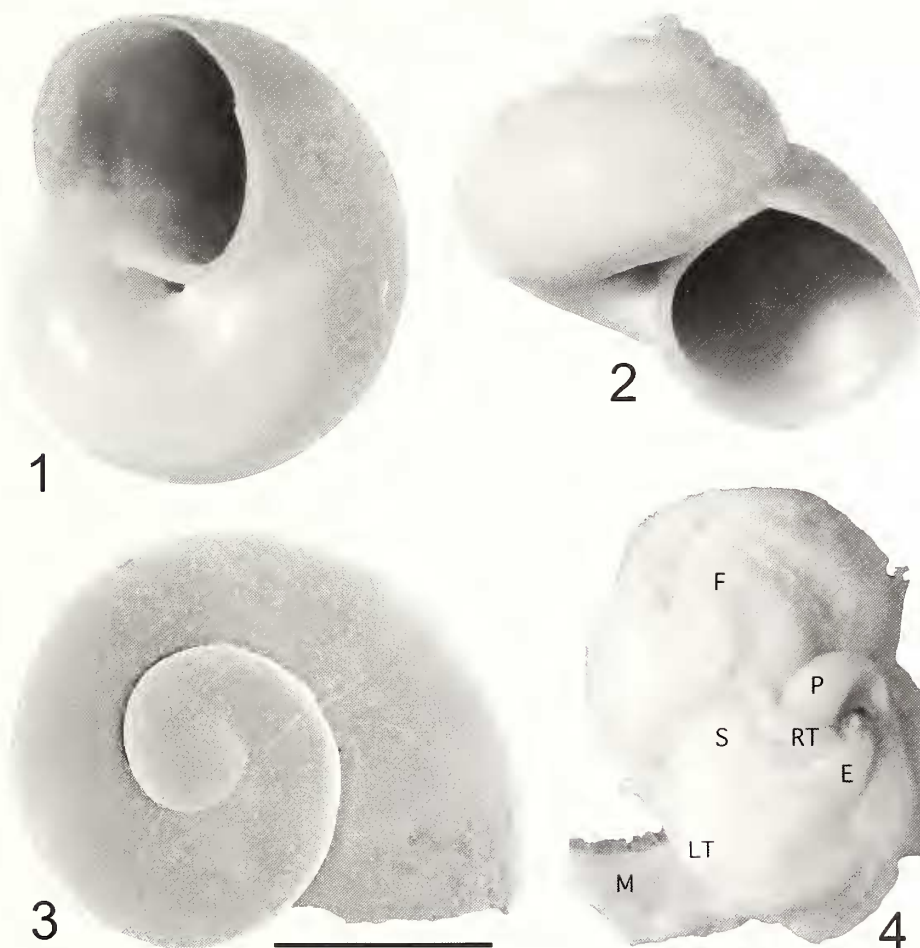
Xeniostoma inexpectans new species

Description: Shell (Figures 1–3): Color silvery white, periostracum fully intact, shiny, thin, tightly adhering; nacre of shell interior strongly iridescent. Shell diameter about 10 mm, whorls 2.7. Whorls rounded but slightly subangulate on shoulder, suture moderately impressed. Surface smooth, axial and spiral sculpture lacking, peristome nearly complete. Aperture large, height of aperture more than half height of shell. Umbilicus narrow, umbilical wall rounded. Height 8.7 mm, diameter 9.4 mm (holotype). Protoconch (Figure 3) smooth, bulbous, about 900 μm in maximum diameter, lip not thickened, transition from protoconch to teleoconch weakly indicated. Operculum corneous, multispiral, about 7 evenly expanding volutions, growing edge fitting the parietal area of the aperture.

**External Anatomy (Figure 4):** Head/foot with evenly tapered suboptic tentacle below right cephalic tentacle and anterior to short eyestalk, contracted length equivalent to that of cephalic tentacle, diameter twice that of cephalic tentacles, not with apparent fold or groove. Tentacle tip tapered. Cephalic lappets lacking, neck lobes of simple narrow flaps. Eyes large, on short stalks, darkly pigmented. Oral disk lacking pseudoproboscis. Anteriormost pair of epipodial tentacles the largest, more posterior pairs small (contracted in preserved specimens). Jaws not detected. Ctenidium bipectinate, free tip short. Osphradium with simple lamellae.

Radula (Figures 5–6): Central field broad, with about 20 pairs of laterals, with inverted-V alignment of tooth rows. Rachidian tooth with tapered tip and broad base. Lateral teeth with broad bases to shafts, tips long and narrow, extending toward rachidian tooth nearly across central field, with deeply serrated edges away from distal end. Extended tips emerging from inner side of tooth base. Basal part of tooth at least four times broader than emerging tip. Lateral edges of tooth bases thin and

Figures 1–4. *Xeniostoma inexpectans* new genus, new species. **1–2.** Holotype, off Kiska Island, Rat Islands, Aleutian Islands, Alaska, 272 m depth, maximum diameter of shell 10.0 mm. **1.** Basal view. **2.** Apertural view **3.** Apical view of immature paratype, showing protoconch and first teleoconch whorl. Scale bar = 1 mm. **4.** Dorsal view of preserved head-foot of holotype, mantle skirt with gill attached (not showing) folded over to left. Abbreviations: LT, left cephalic tentacle; E, eye stalk; F, foot; M, mantle skirt; SO, right suboptic tentacle; RT, right cephalic tentacle; S, snout. Scale bar = 1 mm.
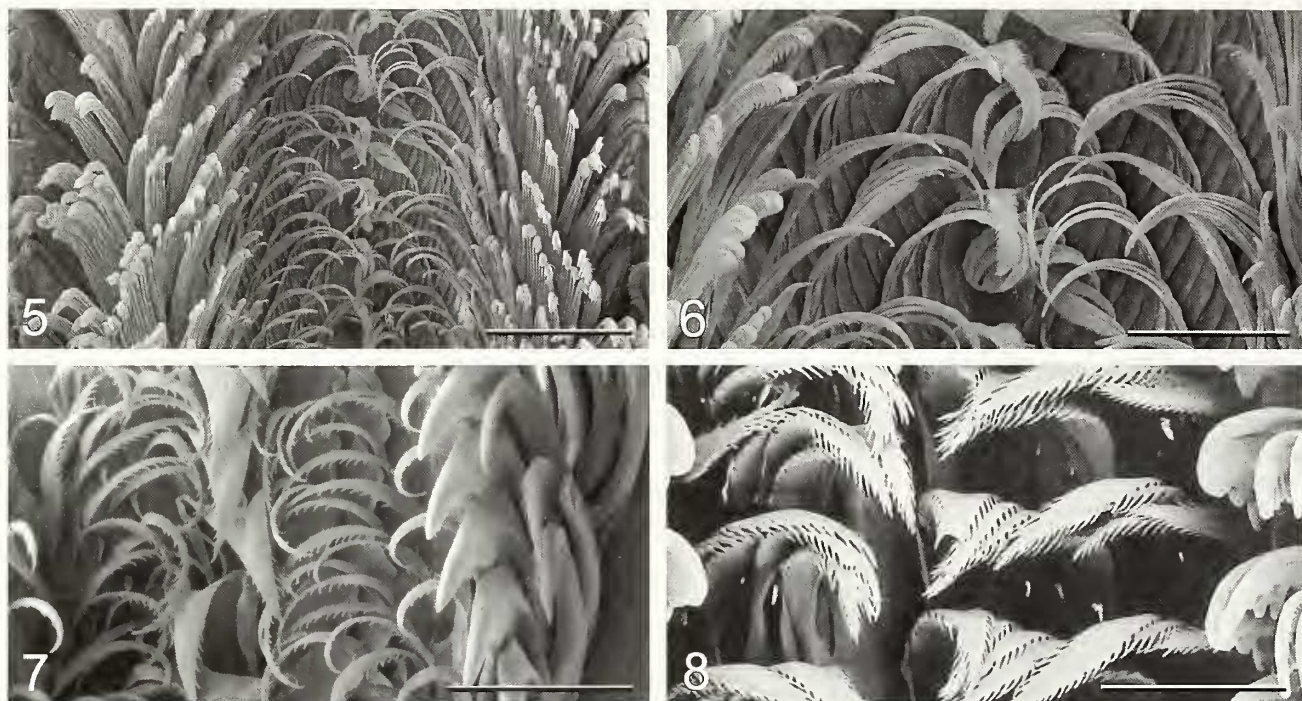
Figures 5–8. Radulae. **5–6.** *Xeniostoma inexpectans* new genus, new species. **5.** Full width of radular ribbon, showing rachidian tooth at center, approximately 20 pairs of curved lateral teeth with broad bases, and numerous, closely adjacent, relatively straight marginal teeth. Scale bar = 200 μm. **6.** Enlarged view of rachidian and adjacent lateral teeth, showing that the rachidian tooth is only slightly broader than adjacent lateral teeth. Scale bar = 100 μm. **7.** *Photinula coerulescens* (King and Broderip, 1831), partial view of ribbon with 4 complete rows of teeth, at center left showing elongate rachidian teeth with long tapering cusps, flanked by four pairs of lateral teeth on left and right; on right showing large inner marginal teeth, and smaller outer marginal teeth (outmost marginals had been stripped away). Scale bar = 200 μm. **8.** *Photinastoma taeniata* (Wood, 1850), central field of radula, showing rachidian and 6 pairs of lateral teeth; on left and right showing enlarged inner marginal teeth and on right showing adjacent lateral teeth. Scale bar = 100 μm. [SEMs, 5–6, D. Geiger, 7. C. Hickman; 8, A. Warén].

flap-like, lacking interlock, concealing inner edge of adja-cent lateral teeth. Marginal teeth numerous, with long shafts and much shorter denticle bearing tips. Inner marginal teeth with short denticles, size of inner marginal teeth not larger than other marginal teeth.

Holotype: LACM 2971 (ex LACM 97-162)

Type Locality: 272 m, W of Kiska Island, Rat Islands, Aleutian Islands, Alaska (51°54.31′ N, 176°35.89′ E), F/V DOMINATOR (sta. 23-971-202), R. N. Clark, 1 August 1997. One live-collected specimen (Figure 1).

Paratypes: LACM 2972 (ex LACM 86-330), 219 m, NE of Semisopochnoi Island, Rat Islands, Aleutian Islands (52°24.09′ N, 179°42.84′ E), Rae Baxter, 10 September 1986; one live-collected specimen and two smaller, dead specimens; maximum diameter 4.8 mm (used for initial radular preparation); one small shell coated for SEM of protoconch (Figure 3); LACM 2973 (ex LACM 97–168), 325 m, SW of Buldir Island, Aleutian Islands (52°18.50′ N, 175°49.0′ E), F/V DOMINATOR (sta. 23-971-243), R. N. Clark, 9 August 1997; 3 spec-imens, 2 live-collected.

LACM 2974 (LACM 97-156), 384 m, SW of Amchitka Island, Rat Islands, Aleutian Islands, Alaska (51° 27.70′ N, 178° 35.0′ E), F/V DOMINATOR (sta. 23-971-181), R. N. Clark, 27 July 1997. 2 live-collected specimens; LACM 3233, 221 m, NW of Kiska Island, Rat Islands, Aleutian Islands, Alaska (52°9.58′ N, 175°11.67′ E), F/V GLADIATOR (sta. 147-04-195), R. N. Clark, 25 July 2004. 7 large spec-imens (1of 3 LACM specimen used for radular SEM, figures 5–6); one paratype, USNM 1184071, and 3 paratypes R. N. Clark Collection.

Distribution and Depth: Rat Islands, western Aleutian Islands, Alaska, from Buldir Island toward the west, to Semisopochnoi Island toward the east, from moderately deep water, depths ranging from 219–384 m. An associ-ation of the new species with vase-shaped hexactinellid sponges of the family Rosellidae has been confirmed, based on the eight additional specimens collected with the sponge from Kiska Island, Aleutian Islands, during the summer of 2004 by Roger Clark.

Etymology: The prefix *xeno* is Greek, *xenos*, a stranger, suggested by the strange combination of characters in the new genus. The root *-iostoma* is based on *Calliostoma*,

the nominate genus of the typical subfamily. The specific name means unexpected.

Comparative Remarks: SHELL. The smooth shell resembles that of the trochid subfamily Margaritinae, particularly the Aleutian Island species *Margarites hickmanae* McLean, 1984, in its large size and silvery white coloration, but differs in its complete lack of spiral sculpture and its larger protoconch size. See McLean (1984) for illustration of *M. hickmanae*.

The smooth shell is unusual for Calliostomatidae; most species of *Calliostoma* and related genera have a high shell profile, often with flat sides. The sculptures of typical species consist of complexly beaded spiral cords. Among the Calliostomatidae, the rounded whorls and the smooth shell of *Xeniostoma* are comparable to the genera *Photinula* (Figures 9–11), which has faint spiral sculpture, and to *Photinastoma* (Figures 12–15), which has more strongly indicated spiral cords in the early teleoconch (Figure 14, 15).

PROTOCONCH. The protoconch at a diameter of 900 µm lacks the typical hexagonal micro-sculpture of most calliostomatids (see Hickman and McLean, 1990, fig. 70D), and is larger than that known for most trochoideans, in which the usual protoconch diameter is about 200–300 µm (Hickman and McLean, 1990). Loss of the hexagonal sculpture would be expected with size increase of the protoconch. The protoconch

of *Photinula coerulescens* is shown here for comparison (Figure 9). It has a diameter of about 500 µm, lacks the hexagonal sculpture and lacks the inflated lip edge. The protoconch of *Photinastoma* is also large, but has broad pits that diminish in size near the edge.

TELEOCONCH I. Marshall (1995: 385, figs. 2–3) indicated that typical calliostomatines have a short segment known as teleoconch I, followed by a growth scar on the first quarter teleoconch whorl, which marks a change to the mature sculpture. This is lacking altogether in *Xeniostoma* (Figure 3), but very faintly indicated in *Photinula coerulescens* (Figure 9), and in *Photinastoma taeniata* (Figure 15).

RADULA. The radula of *Xeniostoma* (Figures 5, 6) has the rachidian and lateral teeth with a long, narrowly constricted upper region of the shaft, with deep serration on the edges, having a strong resemblance to the outer lateral teeth of the calliostomatid genus *Photinula* (Figure 7) and *Photinastoma* (Figure 8), but having a much narrower rachidian tooth and not the enlarged inner marginals. The inner marginal teeth of *Xeniostoma* have the appearance of calliostomatid marginal teeth at the outer zone, but these inner marginal teeth are not enlarged, as in *Photinula* and *Photinastoma*, and all other calliostomatid radulae.

JAW PLATES. Jaw plates in calliostomatids are large, dark brown, and readily observed in preserved specimens through a dorsal cut made on the snout between
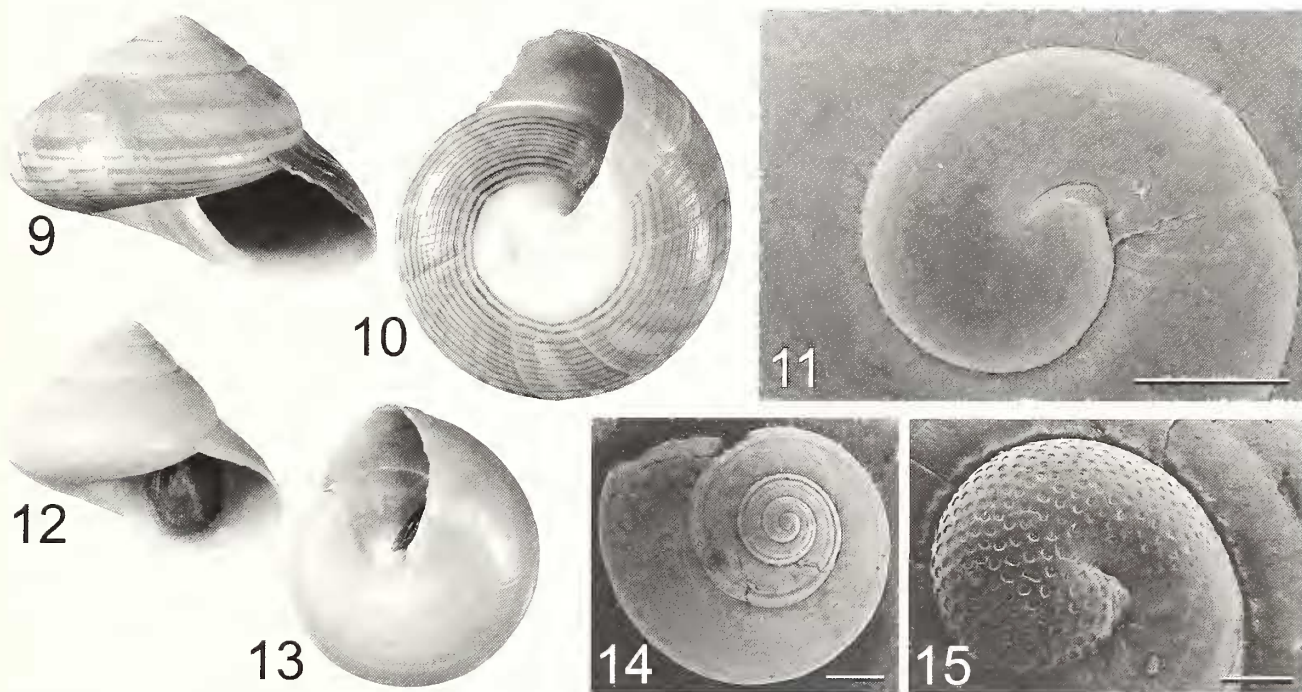
Figures 9–15. Shells and early whorls of *Photinula* and *Photinastoma*. **9–11.** *Photinula coerulescens* (King and Broderip, 1831). **9–10.** Mature shell (LACM 54671), intertidal, Posesion, Chile, height 20.0, diameter 27.9 mm. **9.** Apertural view. **10.** Basal view. **11.** SEM view of apex of small specimen, showing smooth protoconch with pinched tip and lacking apertural rim (LACM 71-30), 75 m, SE of Tierra del Fuego, Chile. Scale bar = 200 µm. **12–15.** *Photinastoma taeniata* (Wood, 1850), Mature shell (LACM 29116), Punta Foca, Puerto Deseado, Argentina, height 9.3, diameter 11.6 mm. **12.** Apertural view. **13.** Basal view. **14–15.** SEM views of apical whorl and protoconch. **14.** Apical whorl. Scale bar 1 mm. **15.** Protoconch. Scale bar = 100 µm. [14–15, SEM by A. Warén].

the cephalic tentacles (see Hickman and McLean, 1990, fig. 68G). No jaws were found for *Xeniostoma*, but the jaws of *Photinula* are large, as in other calliostomatids.

PSEUDOPROBOSCIS. *Xeniostoma* lacks the calliostomatid pseudoproboscis; a pseudoproboscis is present in *Photinula*. The pseudoproboscis of calliostomatids is a shallow groove on the oral disk (see Hickman and McLean, 1990: fig. 70B).

SUBOPTIC TENTACLE. *Xeniostoma* is the first known calliostomatid genus to have a large right suboptic tentacle in mature specimens, as shown in Figure 4. All specimens examined have this structure. This might be construed as a cephalic penis (see Kano, 2008), but it is found on all specimens, which would additionally require the assumption that the species is hermaphroditic. The sex is not known for any of the specimens. The material is not sufficiently well preserved for me to establish a function for the structure, and to establish that the gonad is hermaphroditic. The most likely interpretation (A. Warén, pers. comm.) is that it represents a hyper-development of the anterior right "lateral appendage," of the calliostomatid larval stage, as illustrated by Ramon (1990: fig. 3).

DISCUSSION

Association of Trochiform Vetigastropods with Hexactinellid Sponges: Specimens of *Xeniostoma*, the trochid *Margarella antarctica* (as reported by Gutt and Schicken, 1998), and all species in the family Trochaclididae are associated with glass sponges of the Class Hexactinellida, family Rossellidae (the deep-water vase sponges). The association of *Margarella* and the Trochaclididae are further discussed below.

The most recent general summary of hexactinellid biology is that of Leys et al. (2007). One species of rossellid sponge, *Rhabdocalyptus dawsoni* (Lambe 1892), has been well studied because it accessible to divers off southern Vancouver Island, British Columbia. Studies on the biology of this species are those of Boyd (1981), and Leys and Lauzon (1998), with further details provided by Leys et al. (2007). This species lives at depths below 20 m on the walls of fjords and sloping bottoms below walls of the fjords. Long spicules project beyond the outer wall of *Rhabdocalyptus*, forming a dense veil of spicules that harbors a microfauna of invertebrates (Boyd, 1981), including small crustaceans, polychaetes, small bivalves, and cerithiopsid gastropods, all of which live within the spicule veil for protection from predators and benefit from the flow of particles produced by the pumping action of the sponge. The veil may become clogged with detritus, but the sponge is capable of sloughing off the outer layers of the mat, which is usually accomplished in the winter months.

Another northeastern Pacific genus is *Staurocalyptus*, which produces long spicules that project straight out from the body of the sponge (see *S. solidus* Shulze, 1889, as shown on the cover illustration of Green and Bakus, 1994); the long spicules of this genus also produce a micro-

habitat that provides protections for small invertebrates. According to Reiswig (pers. comm.), the large atrial cavities of rossellid sponges are kept free of sediment by the force of the out-current flow generated by the sponge; these cavities are utilized by larger invertebrates and fishes, and are thus not suitable as a refuge for small gastropods.

Small-shelled vetigastropods of the families Calliostomatidae (*Xeniostoma*), Trochidae (*Margarella*), and Trochaclididae (*Trochaelis*) would be able to find protection from predators within the outer veil of rossellid sponges and would be provided with a continuous flow of detritus. Species in each of these genera are equipped with smooth shells devoid of projecting sculpture, which would enable navigation through a veil or thicket of long, external spicules.

Modifications of the Calliostomatid Radula and Feeding in *Xeniostoma*: Marshall (1995: 386) noted: "As shown by Warén (1990), the calliostomatine radula is distinctive among trochoideans in that the innermost pair of marginals become greatly enlarged at an extremely early stage of ontogenesis, after which the central and lateral teeth arise by intercalation in the central field." The large inner marginal teeth of calliostomatids are also illustrated by Hickman and McLean (1990, figs. 71A, E). It is these enlarged marginal teeth that are the working teeth of calliostomatids, whether feeding on cnidarians or demosponges. Sponge feeding in the non-silicate Demospongia has been infrequently reported in Calliostomatidae (see Marshall, 1988: 228), but there is no previous mention of any member of Calliostomatidae feeding on hexactinellid sponges.

The fact that the innermost marginal teeth of *Xeniostoma* are not enlarged at any stage is a clear indication that this is a radula otherwise unknown in the Calliostomatidae. This indicates that *Xeniostoma* is not carnivorous, as expected in all other calliostomatids. It seems most reasonable that, because *Xeniostoma* does not have any teeth in the radula that are robust enough to function in sponge feeding, the only other option left for such a feathery radula is to assist in feeding on detrital particles, available within the veil of long spicules that project away from the body of the rossellid sponge. There is a source of detritus that settles on hard bottoms in sublittoral zones, in addition to pumping activity of the sponge that would provide a source of detritus flowing toward the outer body wall of the sponge.

Marshall (1995a) considered detritivory to be the mode of feeding in the post-veliger larval stages of calliostomatids. With regard to the termination of the teleoconch I stage at the end of the first quarter of teleoconch growth, Marshall (1995: 385) stated: "It seems clear that the post-larval scar represents a growth pause of a crisis period and I suggest that it may denote the transition to exclusive detritivory (later transitional to carnivory). It may actually mark the transition to carnivory in some species, though the radula may be insufficient to deal with Cnidaria or sponges at such an early stage of development. This interpretation differs from that of

Hickman (1992, fig. 5G), who identified the terminal protoconch varix and the varix following it as denoting the times of hatching and settlement respectively."

Retention of this mode of feeding at maturity is therefore a simple hypothesis for the feeding of *Xeniostoma*. This is confirmed by my finding no sponge spicules in the macerated visceral residue of any examined specimens of *Xeniostoma*.

Egg Size and Protoconch Size in *Xeniostoma*: Males of most species of Calliostomatidae broadcast their gametes, which stimulates females to produce eggs, which are laid in gelatinous strings, with fertilization taking place externally (e.g., Ramon, 1990: 322). Larvae of many species hatch and exit the egg strings as post-torsional veligers (Hickman, 1992). The unusually large protoconch of *Xeniostoma* is indicative of direct development from large, yolky eggs. Relatively few eggs capable of forming a protoconch at such a large diameter of 900 microns could be produced. The veil of spicules on the outer wall of the sponge would provide an ideal site for the early stages of growth in *Xeniostoma*, in affording protection as well as a steady source of detritus.

Loss of the usual micro-sculpture of calliostomatid protoconchs is a function of increased size. Large protoconchs are indicative of large egg size, direct development, and reduced dispersal capabilities. Other large protoconchs lacking the typical hexagonal microsculpture are known in Calliostomatidae; in the deep-sea species *Falsimargarita nanduri* Warén and Bouchet 2001 the 1.2 mm diameter protoconch is smooth (Warén and Bouchet, 2001: 133, fig. 8e).

Feeding in *Margarella Antarctica*: Gutt and Schickan (1998: 403) stated that the Antarctic species "*Margarella* sp. 1" occurs on the glass sponges of the *Rosella/Scolymastra* group, and that "*Margarella* sp. 1 cleans but also feeds on the sponges, thus having both a positive and negative effect on the host." I have not found a detailed account of this relationship in papers cited therein, but the radula of all species of *Margarella* has the rachidian and the lateral teeth with strong cusps (see Zelaya, 2004), so it is conceivable that the teeth of the central field would be capable of feeding directly on the tissue of the hexactinellid sponge, and the marginal teeth would also clean the detritus that accumulates on the sponge.

Feeding in Trochaclididae: The radula of *Acremodonta*, a genus now assigned to the Trochaclididae, was illustrated by Marshall (1983); that of *Trochaclis* was first illustrated with SEM by Warén (1989). These genera have finely divided tips to the numerous teeth, in which the rachidian, laterals and marginals are of similar morphology. The shell of *Trochaclis* species (Figures 17, 10), is much smaller and of higher profile than that of *Xeniostoma*. Here I illustrate the radula (Figure 18) of a yet undescribed species of *Trochaclis*, which shows fully extended lateral teeth with feathery tips. This was prepared by critical point drying of the whole radular ribbon, which provides an improvement over that of most illustrations of the radula of *Trochaclis*, in which the most terminal divisions of the cusps are often clumped together.

All records of trochaclidids indicate an association with hexactinellid, vase-shaped sponges (see Marshall, 1995a), although none of the sponges have been identified in previous accounts. In a review of the species of the southwestern Pacific in the vicinity of New Zealand, Marshall (1995a) stated for the family that "gut contents indicate spongivory." In an effort to confirm this assumption, I examined the macerated viscera of an unnamed species of *Trochaclis* collected from a vase sponge from deep water in the Gulf of Alaska by the late Rae Baxter.
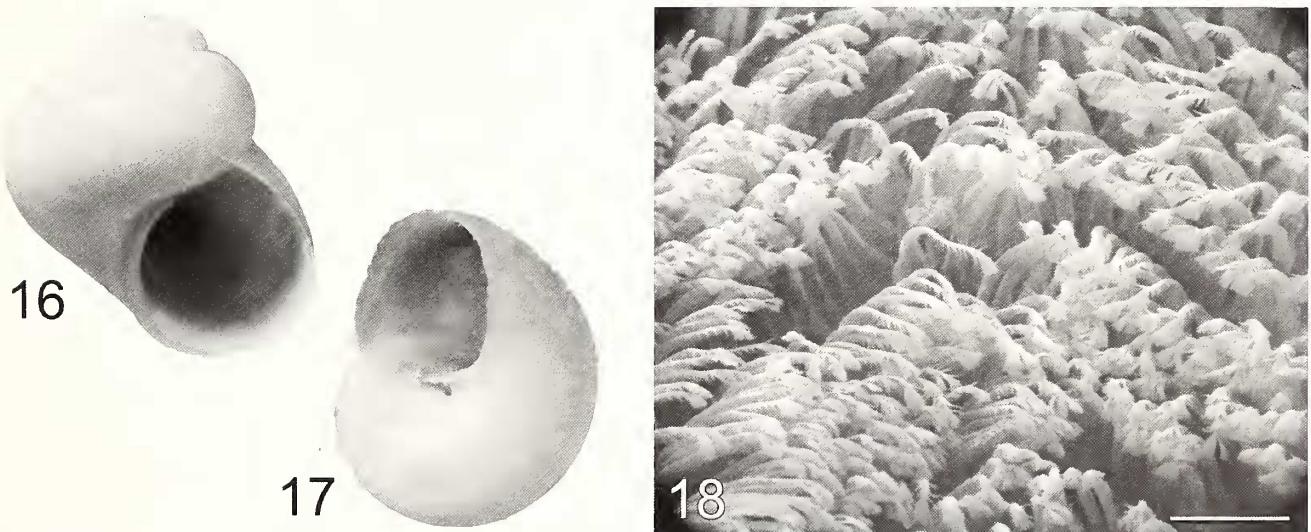
Figures 16–18. Family Trochaclididae, shell and radula of undescribed species of *Trochaclis* from Gulf of Alaska. **16–17.** Shell, height 3.9 mm. **18.** Critical-point dried radula. Scale bar = 20 µm.

I found only a few of the smaller spicules that comprise the body in a rosellid sponge, rather than finding the gut to be packed with sponge spicules. There should be a few spicules that would be shed by the sponge if *Trochaclis* is feeding on detritus, for which its radula is suited. I therefore conclude that *Trochaclis* is also a detrital feeder.

Implications for the Evolution and Higher Classification of Calliostomatidae: Two genera from southern South America, *Photinula* and *Photinastoma*, lack the strongly beaded sculpture of typical calliostomatids, but have other features of typical calliostomatids, including jaws and the pseudoproboscis. Their protoconchs are relatively large; that of *Photinula* (Figure 11) is smooth and that of *Photinastoma* (Figure 15) has pits that suggest a condition comparable to the hexagonal structure of typical calliostomatids with smaller protoconchs. There is early spiral sculpture in the teleoconch of *Photinastoma* (Figure 14). These two genera are therefore retained in the subfamily Calliostomatinae.

Characters of the shell, anatomy, and radula of *Calliostoma* and related genera are sufficiently unlike those of all other trochoideans to justify the family level status currently accepted for Calliostomatidae. On the shell alone, the species of *Calliostoma* in its familiar sense are unlike all other trochoideans in their intricately beaded sculpture and in having the short phase of teleoconch I, representing a suite of characters by which the shell, whether living or fossil, may readily be distinguished from all other trochoideans. These features are so elaborate that they are unlikely to be basal in the family and would have been derived from something much simpler in shell sculpture (Marshall, pers. comm.).

The nearly smooth shell of *Xeniostoma* may well represent a remnant of the basal or stem condition for the family, with shells so unremarkable that there may be a hidden fossil record with unrecognized roots that are deep in geologic time. I am therefore proposing a new subfamily Xeniostomatinae, which could prove to be the basal subfamily for Calliostomatidae, if other genera for living or extinct species are recognized in the future. The other possibility is that all the derived character states of Calliostomatidae have been lost in *Xeniostoma*.

It may be possible to get useful information from molecular sequence information from *Xeniostoma*. If it fits near other species, it is probably a loss of derived characters. If it stands apart, there would be evidence for a deeper division in the family.

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